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Experimental repatriation of snowshoe hares along a southern range boundary reveals historical community interactions

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Abstract

Climate change is altering interspecific interactions globally, yet community-level responses are difficult to predict due to both the direct and indirect effects of changing abiotic and biotic conditions. Snowshoe hares (*Lepus americanus*) are particularly vulnerable to decreasing snow cover and resultant camouflage mismatch. This species shares a suite of predators with alternative prey species including porcupines (*Erethizon dorsatum*) and ruffed grouse (*Bonasa umbellus*), and all three species historically exhibited synchronized population dynamics. Recently, the community has become partially disassembled, notably with the loss of snowshoe hares and associated enemy-mediated indirect interactions resulting from declining snow duration. Specifically, we hypothesized that the extirpation of hares in the early 1990s indirectly increased predation pressure on ruffed grouse and porcupines. To test our hypothesis, we experimentally translocated 96 snowshoe hares to a site within a regional ecotone between northern and southern forests where snowshoe hares were recently extirpated and monitored community members before, during, and after translocation. Ruffed grouse were only loosely associated with the biotic interactions that linked porcupines and snowshoe hares, likely due to predation occurring from avian predators and strong negative direct effects of declining winter snow depths. In contrast, predation of neonate porcupines was virtually non-existent following repatriation, compared with periods without hares. This abrupt attenuation of predation did not increase overall survival due to increased non-predation mortality from cold, early spring weather. Porcupines directly benefited from warming winters: decreased snow cover increased adult survival and warmer temperatures around parturition increased maternal condition and reduced non-predation causes of mortality for neonates. Our experimental manipulation suggests that enemy-mediated indirect interactions were likely to be important features of this community; however, climate change has disrupted these interactions, resulting in extirpation of a central prey species (snowshoe hare) and increased predation of an alternative prey species (porcupine). We show complex effects from climate change with some species directly and negatively affected, while others benefited from direct

effects of warming winters, but suffered negative effects from indirect interactions. Due to absent snowshoe hares and associated biotic interactions, continued persistence of this community module is unlikely, potentially resulting in altered no-analog communities along trailing edge distributions.

INTRODUCTION

Climate change is affecting species unequally (Parmesan et al., 1999; Voigt et al., 2003); some species appear resilient to shifting abiotic conditions, while others are vulnerable to declines, local extirpation, and even extinction (Walther et al., 2002). The varied responses of species to changing climates have reassembled communities into novel and no-analog forms, communities unlike any that currently exist or have historically existed (Williams & Jackson, 2007). While the composition of communities and consequent biotic interactions have long been recognized as drivers of community stability (Hairston et al., 1960; Paine, 1966), they are often overlooked in climate change research (but please refer to Blois et al., 2013; HilleRisLambers et al., 2013; Prugh et al., 2018), even though many of these interactions are climate dependent (Dunson & Travis, 1991; Harley, 2011). For example, experimental studies in Greenland have shown that warming alters forb composition and diversity in Arctic graminoid communities by favoring competitive deciduous shrubs, yet heavy herbivory of shrubs prevents the restructuring of the community (Post & Pedersen, 2008) (although please refer to Boonstra et al., 2018); declines in snow depth reduce winter-killed carrion for scavengers in the Intermountain West of North America, yet wolf-killed (*Canis lupus*-killed) ungulate carcasses can buffer these negative effects of climate change (Wilmers & Post, 2006). Failure to integrate biotic and abiotic factors in predicting the impacts of climate change on community dynamics can result in an inaccurate estimation of current distributions (Araújo & Luoto, 2007; Gilman et al., 2010) and future predictions of range shifts (Engelhardt et al., 2020). Moreover, the rapid pace of climate change has already altered many communities and biotic interactions, which makes the retroactive evaluation of the strength and importance of these interactions unfeasible in many circumstances. Biotic interactions are typically viewed as direct effects, but also manifest as indirect effects, which further complicates the prediction of the outcomes of climate change on community dynamics (Gilman, 2017; Schmitz & Suttle, 2001).

Indirect interactions emerge when the effect of one species on a second is dependent on the presence of a third species (Wootton, 1994). Trophic cascades—a multitrophic interaction driven by the indirect effects of predators on lower trophic levels (Ripple et al., 2016)—are a well documented example of indirect interactions in vertically structured communities (Estes et al., 1998; Post, 2013; Ripple & Beschta, 2012). In laterally structured communities (Post, 2013), enemy-mediated indirect interactions—where the interaction of two or more species of prey are mediated by a mutual predator (Holt, 1977)—are a mechanism by which generalist predators structure prey communities (Holt & Bonsall, 2017). When these interactions result in negative relationships between prey species, it is termed apparent competition (Holt, 1977), and results in dynamics similar to those generated by resource-mediated direct competition (Chaneton & Bonsall, 2000).

Apparent competition can take several forms depending on the functional and numerical response of the predator (Holt & Bonsall, 2017; Holt & Lawton, 1994). When there is no predator preference (i.e., different prey species are equally preferred), prey species have symmetric interactions with their shared predator, which results in negative reciprocal interactions (Holt & Bonsall, 2017). Alternatively, if there is preference for one prey species (e.g., due to lower handling costs or greater caloric benefit), asymmetric competition emerges; here, the abundance of the preferred prey species can increase the abundance of the predator, which will reduce the abundance of the alternative prey species (Chaneton & Bonsall, 2000). Symmetrical relationships then can drive stable coexistence between prey species, while asymmetrical relationships tend to promote declines of the alternative prey species (Chase et al., 2002; DeCesare et al., 2010). However, when the primary prey species competitively excludes alternative prey species, asymmetrical relationships can enable the persistence of alternative prey species (Paine, 1966; Schmitt, 1987). Across shorter time intervals, or when the numerical response of the predator is constrained, functional responses of predators drive prey dynamics to apparent mutualism, in which prey abundances are positively correlated (Holt & Lawton, 1994). Prey switching by predators within the framework of

enemy-mediated indirect interactions can stimulate synchronous population fluctuations of prey communities and even multiyear population cycling (Abrams et al., 1998; Werner et al., 2016). Cyclic dynamics have been theoretically linked to apparent mutualism and competition (Abrams et al., 1998), although the resilience of these cycles under changing enemy-mediated indirect interactions are unknown (Holt & Bonsall, 2017). Because enemy-mediated indirect interactions are difficult to identify in nature due to the complexity of direct and indirect interactions involving multiple species (Gilman, 2017; Holt & Bonsall, 2017), experimental manipulations are a useful framework to test this ecological concept and predict how changing climatic conditions may alter community interactions and dynamics.

Communities existing at the marginal edge of their distribution are particularly vulnerable to the effects of climate change and here is where we may expect to see strong effects of change on biotic interactions (Gosz & Sharpe, 1989; Risser, 1995), as they are likely to include species approaching their thermal (Sunday et al., 2012) and biotic limits (MacArthur, 1972). In the Great Lakes region, the southern range boundaries of multiple species occur along an important transition zone between southern hardwood forests and northern conifer forests (Curtis & McIntosh, 1951). Within this vertebrate community exists a laterally structured community module (i.e., an interconnected subset of species within a community; Gilman et al., 2010) of snowshoe hares (*Lepus americanus*), North American porcupine (*Erethizon dorsatum*) and ruffed grouse (*Bonasa umbellus*) sharing a trophic level and a suite of generalist terrestrial predators including fisher (*Pekania pennanti*), coyotes (*Canis latrans*), and bobcat (*Lynx rufus*), and avian predators including barred owls (*Strix varia*), Great-horned owls (*Bubo virginianus*), and other raptor species (Accipitridae spp.) (Figure 1a). This predator community along the southern range boundary differs from those found at more northern latitudes, most notably by the absence of a specialized hare predator, Canadian lynx (*Lynx canadensis*), whose cyclic population dynamics are linked with those of snowshoe hares (Elton & Nicholson, 1942). Additionally, these terrestrial generalist predators are not specialized for hunting in deep snow depths, having higher foot loading that snow specialists such as Canadian lynx or American marten (*Martes americana*) (Crête & Larivière, 2003; Morin, Bowman, et al., 2020; Suffice et al., 2020). Attenuating snow conditions then may facilitate increased prey access by these generalist predators, who are expanding their geographic range across the Great Lakes region (Crête & Larivière, 2003; Prugh et al., 2009).

Contrastingly, each of the prey species within this module have specific adaptations for persisting in seasonally snow covered landscapes, and changes in climate may affect the population dynamics of each species directly and indirectly through biotic interactions. Ruffed grouse create snow burrows for refuge from predators and cold temperatures; however, if snow is insufficiently deep for burrowing, grouse experience increased mortality (Shipley et al., 2020). Porcupines withstand nutritional restrictions during the winter by catabolizing fat reserves and behaviorally reducing energetic expenditure (Pokallus & Pauli, 2016), yet still pay high fitness costs from both increased predation and energetic costs in deep snow (Mabille et al., 2010). Snowshoe hares experience direct fitness costs from climate change through the mechanism of camouflage mismatch (Wilson et al., 2019; Zimova et al., 2016). Camouflage mismatch in hares occurs when seasonal coat color molts, the timing of which is driven by photoperiod. This no longer coincides with the duration of snow cover on the ground, resulting in increased predation rates when hares are mismatched with their environment (Mills et al., 2013). Camouflage mismatch has been identified as the mechanism driving northward range shifts of snowshoe hare distributions in this region (Burt et al., 2016; Diefenbach et al., 2016; Sultaire et al., 2016; Wilson et al., 2020).

Although the effects of climate change on this community should be strongest along the shared southern range boundary, the geographic range overlap between these species extends across the northern edge of the United States and through much of the forests present in southern Canada and extends across the continent (Figure 1b). Historically, this community of ruffed grouse (Brand et al., 1976) and porcupines (Keith & Cary, 1991) were synchronized with the 10-year population cycle of snowshoe hares (Boutin et al., 1995). Grouse were weakly correlated with the snowshoe hare cycles (Boutin et al., 1995), with peak grouse densities appearing 1 year prior to the snowshoe hare population peak (Keith & Rusch, 1989). Porcupine populations fluctuated cyclically with hares (Figure 1c), yet the mechanisms driving this shared cycling remain completely unknown (Klvana et al., 2004). Interactions between porcupines and snowshoe hares have been well documented, and the presence of snowshoe hares can stabilize porcupine–fisher dynamics (Powell, 1980) and attenuate predation rates for porcupines (Prugh, 2005). Consequently, the climate-driven extirpation of hares has potentially restructured biotic interactions for the remaining community members for which generalist predators dominate.

Following hare population declines, this community module has exhibited signs of change and disassembly: ruffed grouse are exhibiting dampened population cycles (Figure 1c; Williams et al., 2004) and porcupines are experiencing extremely low levels of recruitment from high levels of predation (Pokallus & Pauli, 2015). Additionally, the predator guild of this community has

changed, with fishers recently recolonizing the region, which has contributed to population declines of porcupines (Pokallus & Pauli, 2015). Indications of population declines have occurred synchronously in porcupines and grouse, although the strength of indirect interactions between each of these species and hares may differ. While all three species experience predation from the terrestrial predators, grouse experience more predation from avian predators (Shipley et al., 2020), compared with hares or porcupines (Wilson et al., 2019). Moreover, grouse may experience higher direct costs from climate change, rather than predation, due to increased mortality

in shallow snow (<15 cm; Shipley et al., 2020), compared with when snow is absent or sufficiently deep for burrowing (Shipley et al., 2020). The changes in this community module provide an opportunity to quantify the roles of direct and changing abiotic effects, as well as indirect biotic interactions in structuring dynamics of a prey community featuring different strengths of interactions and sensitivity to climate change.

To test hypotheses about the role of enemy-mediated indirect interactions in structuring a community of vertebrates and disentangling the effect of climate change on these biotic interactions, we experimentally manipulated a long-term study site along this southern range boundary by translocating snowshoe hares back into a system from which they were recently extirpated due to climate change. Our objective was to temporarily resurrect historical population dynamics and community interactions, and determine the role of hares, and their population dynamics, in regulating predation of alternative prey species in a multiprey, shared-predator community module. To reconstruct historical interactions and identify enemy-mediated indirect interactions for this community we quantified the demographic response of alternative prey species to the experimental repatriation, the releasing of individuals of a native species to an area currently or formerly part of its historic range (Dodd Jr. & Seigel, 1991),
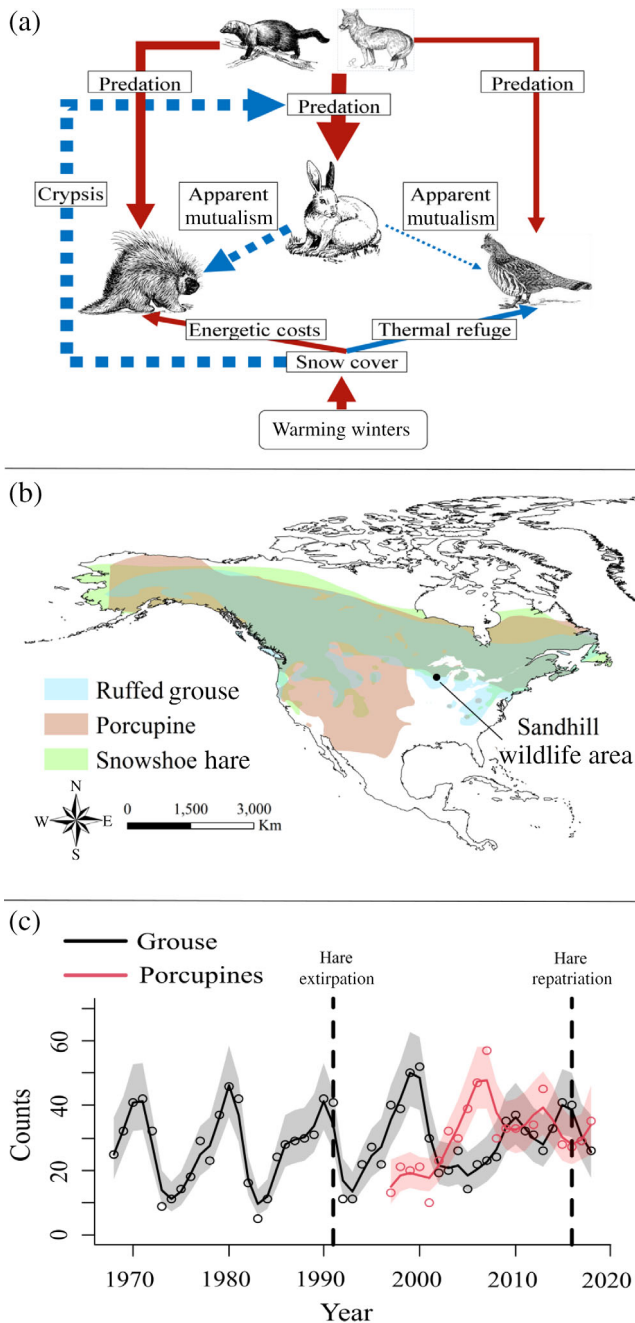

FIGURE 1 (a) Hypothesized relationships (positive, blue line; negative, red line; direct relationships, solid arrows; indirect relationships, dashed arrows) between alternative prey species North American porcupine (*Erethizon dorsatum*), snowshoe hares (*Lepus americanus*), and ruffed grouse (*Bonasa umbellus*); and shared predators fisher (*Pekania pennanti*) and coyotes (*Canis latrans*) mediated by abiotic and biotic factors. Thickness of the lines represents the relative strength of interaction compared with other species. (b) Distribution ranges for porcupines (Emmons, 2016), ruffed grouse (BirdLife International, 2018), and snowshoe hares (Mills & Smith, 2019), showing extensive spatial overlap between species across the boreal forest. Our study site along the southern range boundary of all three species is indicated. Range data were obtained from the IUCN RedList, and were modified to reflect current porcupine range boundaries in Wisconsin and Michigan (GBIF.org, 2021). (c) Population trends for focal species within Sandhill Wildlife Area between 1968 and 2018. While ruffed grouse continued to decline following hare repatriation, porcupines showed a slight increase. Actual census counts for ruffed grouse drumming surveys (black shaded area) and porcupine winter captures (red shaded area) are represented by open circles. Solid lines indicate population trends, estimated using a generalized additive model from count data (Wood, 2006), with shaded areas indicating 95% confidence intervals. Dashed lines indicate hare extirpation and translocation, taken from Keith et al. (1993) and Wilson et al. (2019)

of snowshoe hares to this community module. We hypothesized that enemy-mediated indirect interactions linked the population dynamics of prey species when snowshoe hares were extant on the landscape. We predicted that the presence of snowshoe hares would increase survival in porcupines, especially the most vulnerable age class (neonates) and increase survival in ruffed grouse, although the effect would be lessened in grouse due to incomplete sharing of predators. Additionally, we predicted that climate change would have direct effects on prey vital rates, with declining snow conditions positively affecting porcupines and negatively affecting grouse. To understand the forces governing this historical community and to predict how this community may operate in the future under very different climatic and biotic conditions we combined long-term demographic data with an experimental framework to restore historical biotic interactions in a community that was experiencing rapid changes in abiotic conditions.

METHODS

Study area

Sandhill Wildlife Area (from this point forwards Sandhill; 44.307° N, 90.129° W) is a 3700 hectare property owned and managed by the Wisconsin Department of Natural Resources and situated within the "ecological tension zone" of Wisconsin (Curtis & McIntosh, 1951). Historically, Sandhill and the surrounding regions were agricultural lands until the Great Depression in the United States in the 1930s, when it was purchased as a wildlife game farm and enclosed by a nine-foot fence to retain white-tailed deer (*Odocoileus virginianus*) within the property. Currently, Sandhill is part of a complex of State and county wildlife areas across the region connecting Sandhill to other natural areas including Necedah National Wildlife Refuge and Meade State Wildlife Area, with private residential areas and cranberry farms interspersed (Wisconsin DNR, 2011). Upland habitats make up ~52% of Sandhill, predominately consisting of aspen (*Populus* spp.) and oak (*Quercus* spp.) forest with interspersed pockets of jack pine (*Pinus banksia*), red (*Pinus resinosa*) and white pine (*Pinus strobus*), and black spruce (*Picea mariana*), with open wetlands comprising the remainder of the area (Keith et al., 1993). Snowshoe hare population dynamics were cyclic in Wisconsin until the 1950s (Keith, 1963), and thereafter fluctuated irregularly (Buehler & Keith, 1982). Populations of hares were historically present at Sandhill, with densities of 0.4/hectare reported in the early 1980s (Kuvlesky & Keith, 1983); however, by the late 1980s populations had declined and hares had become functionally extirpated in Sandhill by the early

1990s (Keith et al., 1993). Several long-term ecological studies have been conducted at Sandhill, focusing on the historical population dynamics of snowshoe hares (Buehler & Keith, 1982; Kuvlesky & Keith, 1983; Sievert & Keith, 1985), demographics and habitat selection of ruffed grouse (Kubisiak, 1985; Shipley et al., 2019), and current predator–prey dynamics (Pokallus & Pauli, 2015, 2016).

Between 16 January and 16 February 2017, we opportunistically trapped 96 snowshoe hares from a large population of hares in the Chequamegon National Forest Medford District (45.92008° N, 90.4518° W) using livetraps (Type 205, Tomahawk Live Traps, Tomahawk, WI). Hares were weighed, identified to sex, and fitted with radiocollars (M1575, Advanced Telemetry Systems, Isanti, MN), then transported 137 km south to Sandhill in a secured pet carrier. Once at Sandhill, we held hares in one of three temporary holding pens (Figure 2), enriched with woody debris for cover and food, for two nights as part of a "soft release" aimed to increase female survival and decrease dispersal distance following release (Letty et al., 2000). Release sites were selected based on their proximity to high-quality hare habitat and their proximity to areas where monitoring of porcupines and ruffed grouse was active (Figure 2). All releases occurred in the southern half of Sandhill to co-occur with the long-term monitoring of porcupines (Figure 2). Hares were monitored through December 2018 when the final radiocollar died. Further details on hare translocation can be found in Wilson et al. (2019, 2020). Long-term monitoring of both porcupine and ruffed grouse at Sandhill occurred from 1997 to 2018 and from 1968 to 2018, respectively. We counted porcupines in the winter by capturing and marking detected individuals, while grouse were monitored using drumming surveys in April of each year. Drumming surveys were conducted by Wisconsin Department of Natural Resource personnel and consisted of systematic dawn auditory surveys for drumming individuals. Once a drumming individual was detected, the drumming log was identified and location recorded (Gullion, 1966). We used a generalized additive model to visualize population trends from these count data and compare population trends following hare repatriation (Figure 1b).

Data collection

Ruffed grouse

We trapped grouse using walk-in pens connected by a drift fence (Gullion, 1965) between September and November in 2015–2017. We determined age and sex of each grouse by feather molt patterns of wings and tails, respectively (Hale et al., 1954), and fitted individuals with
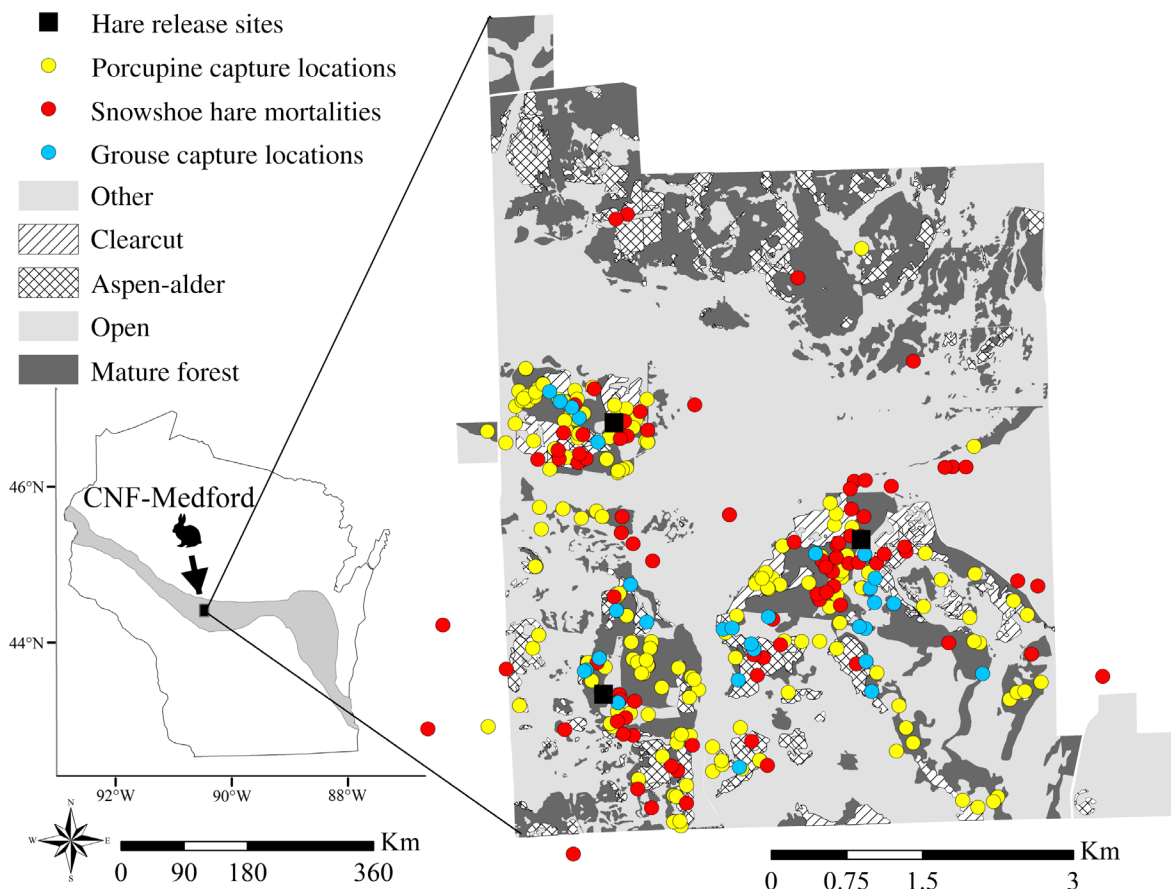
FIGURE 2 Map indicating the locations of source populations of snowshoe hares for the translocation to Sandhill Wildlife Area. The shaded area indicates Sandhill's location within the ecological tension zone (Curtis & McIntosh, 1951), while the hare icon indicates the approximate location of the source population in the Chequamegon National Forest. Inset shows the extent of spatial overlap of snowshoe hares (*Lepus americanus*), porcupine (*Erethizon dorsatum*), and ruffed grouse (*Bonasa umbellus*) used in this study, indicating potential for biotic interactions between these species

VHF radiotransmitters equipped with 4-h mortality sensors (Advanced Telemetry Systems, Isanti, MN). During winters (1 December to 31 March), we scanned for mortality signals every 2 days; during spring (1 April to mid-June) and fall (mid-June through September) checks were conducted twice a week and once a week, respectively. Upon detection of a mortality signal, we collected remains, and identified causes of mortality, as well as the predator responsible, when possible. Grouse were monitored through August 2018. Further details on ruffed grouse capture and monitoring can be found in Shipley et al. (2019, 2020).

Porcupine

From 1997 through 2018, except during 2011 and 2014, we conducted an annual winter trapping survey of porcupines Sandhill beginning in January and extending through mid-April. Porcupines spend winter, a time of resource limitation and energetic deficits, in mature forests using natural shelters such as tree cavities and rocks

as thermal refugia from cold winter temperatures, emerging typically at night to feed on bark and twigs (Roze, 2009). We located porcupines by searching for signs such as tracks, scat, or evidence of feeding in trees and tracked individuals back to denning sites. Porcupines were captured using a box trap (DS100 and 1082SS; Tomahawk Live Trap, Tomahawk, WI) placed over the den opening. Traps were wrapped with a tarp and straw for insulation, provisioned with apple slices and alternative exits were blocked with sticks or other debris. Traps were set in the afternoon and checked in the morning; individuals were captured typically within the first night of trapping. Porcupines were transported to a covered garage for processing, for which they were sedated with an intramuscular injection of Telazol (Hale et al., 1994). Once sedated, porcupines were aged by dentition into juvenile (<1 year), subadult (1–2 years), or adult (2+ years) age classes (Earle & Kramm, 1980), and sexed by palpation anterior to the genital opening (Roze, 2009). We injected all new captures with a PIT tag (AVID Friendchip; AVID Identification Systems, Norco, CA) for identification. Individuals were weighed in all years and

morphometric measurements were collected in 2012–2018. In 2012 and 2015–2018, adult females were fitted with VHF radiocollars equipped with 8-h mortality sensors (M2930B; Advanced Telemetry Systems, Isanti, MN).

Porcupines breed in the fall (September/October) and carry a single offspring to term overwinter until they give birth in the spring (mid-April) (Roze, 2009). Beginning in mid-April, we relocated radiocollared females and searched for offspring. By spring, females had abandoned their winter dens and moved into areas with more ground cover to give birth (Pokallus & Pauli, 2015). Neonates were typically found in proximity to females, and the presence of a female on the ground was a good indicator that a neonate was nearby. Discovery of a neonate offspring was our primary method of confirming the reproductive status of a female. If we were unable to confirm pregnancy, we recaptured females in May and assessed reproductive status by palpation and sonography. If palpation and sonography yielded a negative result, the female was given a dose of oxytocin, which would stimulate lactation in a female who had given birth already (Roze, 2009). Initial detection was defined as the first date at which we discovered a neonate. Upon detection of a neonate porcupine, we weighed and identified the sex of the individual and injected a PIT tag. We visually checked these individuals daily to measure survival until they reached 1 kg in weight when they were implanted with an intraperitoneal VHF transmitter (IMP-130; Telonics, Mesa, AZ). To minimize human disturbance around birth sites, visual checks were performed at a distance with binoculars, when possible, and different routes to the birth site were taken daily. Following implantation, we allowed neonates to recover overnight, and released them at the site of capture. Neonates were checked daily for survival until mid-June and then at weekly intervals afterwards until January when they were eligible to be captured in surveys. Upon detection of a mortality signal we investigated the kill site, and identified causes of mortality and identities of the predator using the available signs. All handling and processing methods conformed to the American Society of Mammalogists' guidelines (Sikes et al., 2011) and were approved by the University of Wisconsin-Madison Institute for Animal Care and Use Committee (IACUC) (protocol A005849).

Data analysis

Variable selection

We used a shared group of variables to test hypotheses of the direct effects of winter weather and repatriation of snowshoe hares on survival of adult, subadult, and juvenile porcupines and ruffed grouse. Variables included sex, age class, temperature, snow duration, and hare presence. We characterized age class as adult, subadult, or juvenile for porcupines and juvenile or adult for ruffed grouse based on whether a bird had hatch-year or after-hatch-year plumage at capture. Temperature was characterized as the mean minimum temperature between 1 December and 31 March for porcupines and each week for grouse. We characterized snow duration as the difference between the first day of the first continual 14-day stretch of snow cover (initiation) and the last day of the last continual 14-day stretch of snow cover (termination) in a season (Sultaire et al., 2016) for porcupines and defined this as a binary variable for grouse, indicating whether the week fell between initiation and termination dates of snow cover. For both porcupines and grouse, we characterized the presence of hares as a binary variable, indicating whether the period occurred after the translocation. Data on snow cover and nightly temperature were obtained from the Wisconsin Rapids Grand Ave B station (Menne et al., 2012).

Survival modeling

We compared weekly survival for ruffed grouse using a binomial known-fates framework in the R package *RMark* (Laake et al., 2019). Survival models included individual covariates for sex and age class and environmental site-variables temperature, snow duration, and hare presence. Weekly survival estimates were converted to seasonal estimates by taking the product of estimates across the appropriate period and variances were estimated using the delta method.

We estimated apparent survival (Φ) and probability of recapture (p) of porcupines from annual survey recapture data using Cormack–Jolly–Seber mark–recapture models in the R package *RMark* (Laake et al., 2019). Models for p included site-level variables for temperature, snow duration, and fully time-dependent models in models. Models estimating Φ included sex and age class included as grouping variables, and annual site-level covariates for temperature, snow duration, presence of snowshoe hares, and fully time varying models. We assessed model fit and checked for evidence of overdispersion (Fletcher, 2011). We conducted model selection using a secondary candidate approach (Morin, Yackulic, et al., 2020). We first ran all p candidate models holding Φ as the null model, then ran all Φ candidate models, holding p as the null model. We then took all candidate models from both parameters within 10 AIC$_c$ of the top model and included them in a second set of candidate models comprised of all combinations from the initial model selection. All models were ranked using AIC$_c$, and the importance of variables was evaluated using 95% confidence intervals.

Recruitment

Because we lacked data on clutch size, hatch success, and chick survival, we did not estimate recruitment parameters for ruffed grouse. Estimation of recruitment parameters for porcupines began by calculating survival of neonates for each year using a Kaplan–Meier framework. We defined causes of mortality as either predation or non-predation mortalities. Non-predation mortalities were not always identifiable by cause, but included stillbirths, exposure, and other causes in which the carcass was recovered intact. We used a competing risks framework with non-parametric cumulative incidence functions to estimate cause-specific mortality rates (Murray & Patterson, 2006). We pooled samples into years before the translocation (no hares) and years following the translocation (hares). Cumulative incidence functions were estimated using the R package *cmprsk* (Gray, 2004). We used Cox proportional hazard models in the R package *survival* (Therneau & Lumley, 2014) to evaluate risk factors for cause-specific mortality. Risk factors included individual covariates for sex, maternal condition, precipitation, winter NAO, temperature, Julian date of vegetation emergence, Julian date of vegetation senescence, snowfall, and growing degree-days. Maternal condition for each neonate was estimated from the capture records of its parent and was represented as the conditional residual from a mixed-effects regression of hindfoot length and Julian date and the random effect of parent (Schulte-Hostedde et al., 2005). Precipitation, growing-degree-days, and temperature were defined as the total non-snow precipitation, total growing-degree-days and mean minimum nightly temperature respectively from the 7 days prior to and following the initial discovery of the neonate. Vegetation emergence was defined as the number of days between initial discovery and the start of season time for that year, while vegetation senescence was defined as the number of days between the end of season time for the previous year and discovery date. Start of season and end of season time are metrics indicating the start of the growing season and end of the growing season, respectively, based on the Normalized Difference Vegetation Index and were obtained from the USGS/EROS Center (U.S. Geological Survey, 2019). Data for precipitation, growing-degree-days, and temperature were obtained from weather station data from the National Climatic Data Center (Menne et al., 2012).

Additionally, we performed a post hoc analysis to determine the drivers of maternal condition. We used a general linear regression model to test the effects of seasonal drivers on maternal condition. We considered site-level variables representing snow initiation from the year of capture, growing season duration, and previous winter's snow duration. Snow initiation was the Julian date of the first day of the first continuous 14-day period of snow cover. Growing season duration was the difference between start of season time and end of season time at Sandhill from the previous summer. Previous winter snow duration was calculated identically to the methods used in the mark–recapture analysis.

Population modeling

We focused on the population trajectories of porcupines given their notable response to hare repatriation. Specifically, we compared the relative effects of changing climate and hare presence on porcupine population size by running population projections of scenarios with a 2×2 design, incorporating scenarios with and without hares and individuals experiencing historical snow conditions from 1971–1990 and future climate conditions from 2040–2059. We estimated mean snow duration, mean snow initiation date, and mean snow termination date for both historical and future periods. Historical snow data were obtained from weather stations near Sandhill (Menne et al., 2012). Future snow cover data were calculated based on ensemble median snow cover from nine models for an A2 emissions scenario (Notaro et al., 2014; Sultaire et al., 2016). We designed a three-stage female-only Leftkowich population matrix model (Caswell, 2000) for porcupines in Sandhill using data from the mark–recapture and cumulative incidence functions to populate the model (Figure 3). Transition probabilities between juvenile, sub-adult, and adult age classes were estimated using the top model from the Cormack–Jolly–Seber mark–recapture probabilities, including environmental stochasticity when appropriate. Recruitment (m_3) was calculated as the product of the proportion of pregnant females in the population and neonate survival from initial discovery through 31 December, when they were available to be captured in winter surveys. We calculated the proportion of adult females who bred by dividing the total number that showed evidence of reproduction by the total numbers of adult females captured. We used a constant value across all scenarios to represent the proportion of pregnant females; but survival of neonates incorporated environmental stochasticity and its effects on maternal condition and the resulting neonate survival. Additionally, we explored neonate survival three different ways. First, we only considered predation-related mortality and used the cumulative incidence function for predation mortality in hare and non-hare scenarios and under historic and future climatic conditions. These scenarios incorporated environmental stochasticity by varying snow duration using a Monte Carlo estimator drawing from a normal

distribution of current and historic snow duration records (Figure 3). Next, we held predation-related mortality constant and compared non-predation-related mortality between historic and future climatic conditions. These scenarios incorporated environmental stochasticity in age class transition parameters (Figure 3), but also incorporating changes in maternal condition and neonate survival by snow initiation dates and previous winter duration. However, because hare presence only affected predation hazard rates, scenarios with and without hares were identical. Finally, we combined cumulative incidence functions for predation and non-predation mortality additively and considered this the realistic effect of translocation and changing climate on porcupine population projections. These scenarios incorporated environmental stochasticity identically to non-predation scenarios, but predation mortality was additively included to the non-predation hazard rate. We used an initial starting population of 31 adults, four subadults, and three juveniles, which represented the minimum female population of porcupines from the final year of surveys (2018). We ran 500 simulations of each scenario for a duration of 30 years. Additionally, we estimated λ, sensitivity, and elasticity (Caswell, 2000) for scenarios with or without hares, holding snow duration at mean values using the R package *popbio* (Stubben et al., 2020).

RESULTS

Long-term monitoring

Ruffed grouse drumming surveys exhibited a 10-year population cycle, although these cycles have dampened in amplitude in recent years (Figure 1c). Porcupines showed an initial increase in abundance, followed by a population decline at least partially driven by the recolonization of fishers in the mid 2000s (Pokallus & Pauli, 2015). Although we lacked data on porcupines immediately following hare extirpation, grouse showed little response to hare extirpation. Following the experimental repatriation of hares to Sandhill, the total numbers of porcupines increased, whereas grouse populations declined (Figure 1c).

Ruffed grouse

Between September 2015 and August 2018, 59 ruffed grouse were captured and radiotagged in Sandhill Wildlife Area. There were 41 mortality events across these years, with predation ($n = 32$) as the primary cause of mortality. Survival analysis using known-fate models indicated that intrinsic factors, specifically sex and age
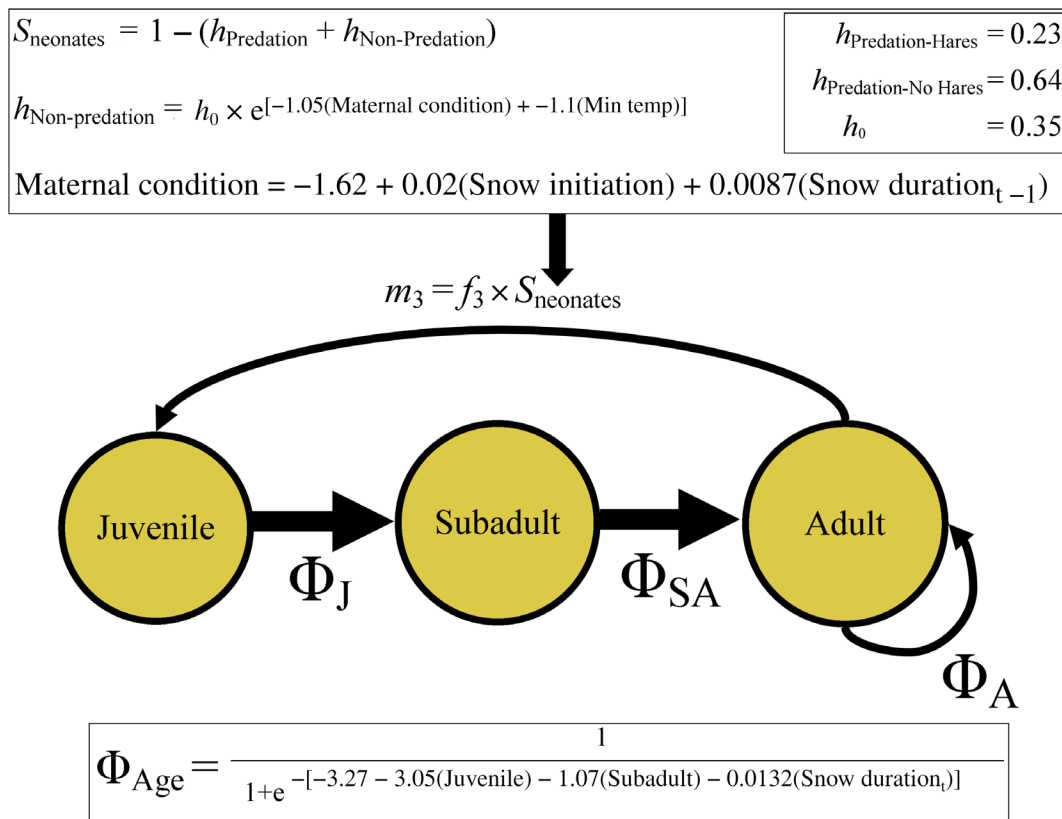

$$S_{\text{neonates}} = 1 - (h_{\text{Predation}} + h_{\text{Non-Predation}})$$

$$h_{\text{Non-predation}} = h_0 \times e^{[-1.05(\text{Maternal condition}) + -1.1(\text{Min temp})]}$$

$$\text{Maternal condition} = -1.62 + 0.02(\text{Snow initiation}) + 0.0087(\text{Snow duration}_{t-1})$$

$h_{\text{Predation-Hares}}$	$= 0.23$
$h_{\text{Predation-No Hares}}$	$= 0.64$
h_0	$= 0.35$

$$m_3 = f_3 \times S_{\text{neonates}}$$

$$\Phi_{\text{Age}} = \frac{1}{1 + e^{-[-3.27 - 3.05(\text{Juvenile}) - 1.07(\text{Subadult}) - 0.0132(\text{Snow duration}_t)]}}$$

FIGURE 3 Life cycle diagram for porcupines (*Erethizon dorsatum*) in Sandhill Wildlife Area between 1997 and 2018, with equations used to calculate respective transition parameters

class, are stronger predictors of survival in ruffed grouse than the presence of hares on the landscape. The top-ranked model indicated that males had higher survival rates than females ($\beta = 0.82$, 95% CI = 0.14, 1.50) and juveniles had higher survival than adults ($\beta = 0.62$, 95% CI = −0.20, 1.45). Multiple other models were competitive with the top model including the null model ($\Delta AIC_c = 1.21$), but the coefficient confidence intervals (CI) for hare presence overlapped zero in all models, suggesting that it was uninformative (Appendix S1: Table S4).

Porcupine

Annual porcupine captures in the census varied between 10 and 57 individuals. Females had a higher probability of recapture than males ($\beta = -0.55$, 95% CI = −1.00, −0.096) and the increased duration of snow cover led to a lower probability of recapture ($\beta = -0.011$, 95% CI = −0.017, −0.0042). Temperature was also included in competitive models (<2 AIC_c) for p, along with sex and snow duration (Table 1), but the confidence interval overlapped zero and was deemed uninformative (Arnold, 2010). Females had a higher probability of survival than males ($\beta = -0.79$, 95% CI = −1.19, −0.38), whereas adults had a higher survival than either juveniles

($\beta = -3.05$, 95% CI = −3.84, −2.26) or subadults ($\beta = -1.07$, 95% CI = −1.90, −0.24). Additionally, increased snow duration led to decreases in survival ($\beta = -0.013$, 95% CI = −0.028, −0.001; Figure 4a).

Although we found a large amount of variation in survival for neonates, there was no evidence of a difference between years with hares ($\widehat{S}_{2012} = 0.10$, 95% CI = 0.026, 0.40; $\widehat{S}_{2015} = 0.0$; $\widehat{S}_{2016} = 0.35$, 95% CI = 0.17, 0.71) and those years without hares ($\widehat{S}_{2017} = 0.33$, 95% CI = 0.15, 0.73; $\widehat{S}_{2018} = 0.43$, 95% CI = 0.026, 0.40). Notably, however, neonate cause-specific mortality differed between years with hares and those years without hares (Figure 4b). Predation mortality was high ($h_{Pred} = 0.64$, 95% CI = 0.61, 0.67) and non-predation mortality was low ($h_{Non\text{-}Pred} = 0.14$, 95% CI = 0.12, 0.16) in years without hares, yet this reversed following the translocation with non-predation mortality high ($h_{Non\text{-}Pred} = 0.40$, 95% CI = 0.36, 0.43) and predation mortality low ($h_{Pred} = 0.23$, 95% CI = 0.21, 0.26) (Figure 4c). Neonates born from females in poorer condition (Odds Ratio [OR] = 0.35, 95% CI = 0.11, 1.12) and experiencing lower mean minimum temperatures (OR = 0.33, 95% CI = 0.15, 0.76) were more likely to experience non-predation mortality. We estimated the baseline hazard rate for non-predation mortality to be 0.35 and used this value to estimate hazard rates, accounting for the effect of environmental stochasticity (Figure 3). Our post- hoc analysis of

TABLE 1 Model selection results for survival of porcupines (*Erethizon dorsatum*) at Sandhill Wildlife Area from 1997–2018 using Cormack–Jolly–Seber mark–recapture analysis

	Model	k	AIC_c	ΔAIC_c	w_i
p	Phi(.)p(Sex + Snow)	4	1593.25	0.00	0.35
	Phi(.)p(Sex + Temp + Snow)	5	1593.51	0.27	0.31
	Phi(.)p(Sex + Temp)	4	1594.01	0.78	0.24
	Phi(.)p(Sex × Temp)	5	1595.96	2.71	0.09
	Phi(.)p(Sex)	3	1600.23	6.99	0.01
Φ	Phi(age + Sex)p(.)	5	1520.58	0.00	0.40
	Phi(age + Sex + Snow)p(.)	6	1521.76	1.18	0.22
	Phi(age + Sex + Temp)p(.)	6	1522.55	1.97	0.15
	Phi(age + Sex + Hares)p(.)	6	1522.61	2.03	0.15
	Phi(age + Sex + Snow + Hares)p(.)	7	1523.81	3.23	0.08
2° Candidate	Phi(age + Sex + Snow)p(Sex + Snow)	8	1510.44	0.00	0.19
	Phi(age + Sex + Snow)p(Sex + Snow + Temp)	9	1510.95	0.51	0.15
	Phi(age + Sex)p(Sex + Snow)	7	1511.97	1.54	0.09
	Phi(age + Sex)p(Sex + Temp)	7	1512.27	1.84	0.08

Note: We tested for the effects of snow duration (Snow), mean minimum temperature between 1 December and 31 March (Temp), presence of snowshoe hares (*Lepus americanus*; Hares), and sex. Models <10 ΔAIC_c from the top model are included for initial phases (p[detection] and Φ[apparent survival]), while only models within 2 ΔAIC_c are shown for the secondary candidate set.

Abbreviations: ΔAIC_c, difference in AIC_c from top model; AIC_c, Akaike's information criterion corrected for small sample size; k, number of parameters; w_i, AIC_c model weight.
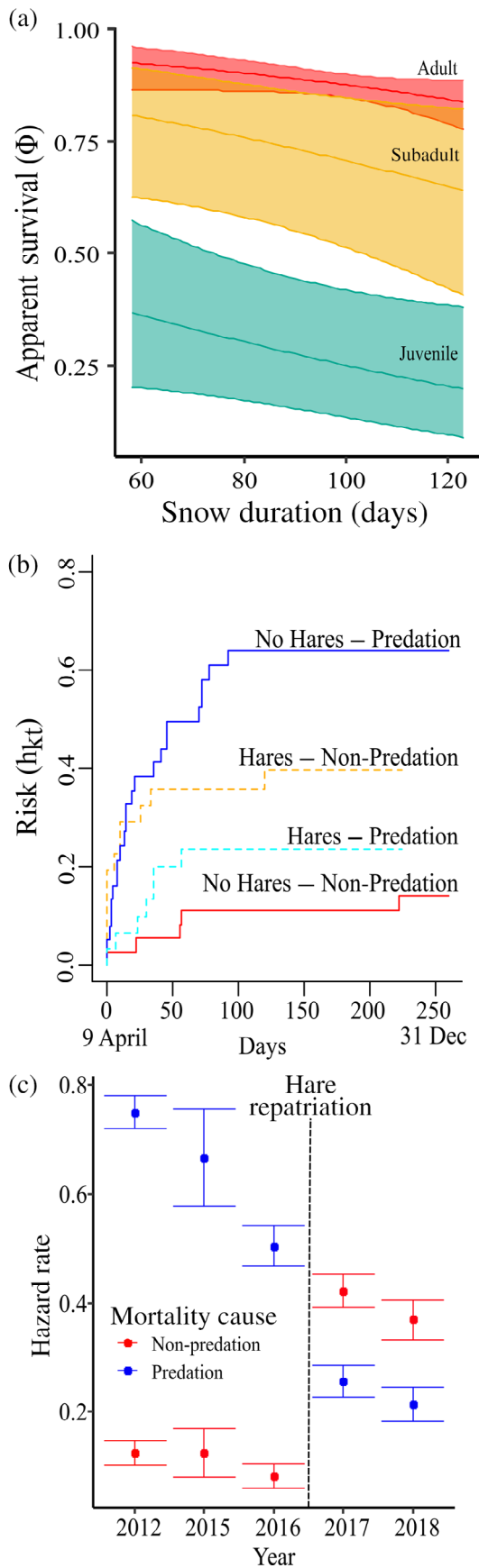
predictors of maternal condition indicated that initiation date of snow cover ($\beta = 0.021$, 95% CI = 0.008, 0.033) and duration of previous winter ($\beta = 0.009$, 95% CI = −0.001, 0.018) were the strongest predictors of maternal condition (Appendix S1: Table S3).

Porcupine populations were declining under both scenarios with hares ($\lambda = 0.96$, 95% CI = 0.91, 1.00) and without hares ($\lambda = 0.92$, 95% CI = 0.88, 0.95), assuming no immigration. Adult survival was the most sensitive and elastic transition for both scenarios. Porcupine populations declined regardless of climatic conditions or the presence of snowshoe hares, however projections with only the predation hazard rate showed the largest differences between scenarios with hares and those without (Figure 5a). The presence of hares resulted in higher mean final population sizes under both future climatic conditions ($N = 11.81$, SD = 6.24) and historical climatic conditions ($N = 7.10$, SD = 4.37), compared with the scenarios without hares for both historical ($N = 2.23$, SD = 1.99) and future climate conditions ($N = 2.42$, SD = 2.13) (Figure 5a). There were minimal differences in final population size when isolating the non-predation component and comparing future ($N = 5.18$, SD = 3.53) and historic ($N = 3.05$, SD = 2.81) scenarios, and when comparing scenarios including both predation and non-predation components of mortality (Figure 5b). Despite the lack of difference in means, all scenarios in which hares were present had a larger proportion of simulations in which final porcupine populations were greater than a quasi-extinction threshold of 10 individuals compared with scenarios without hares (Figure 5b), indicating increased potential for persistence when hares are present on the landscape, and the importance of biotic interactions in porcupine demographics when compared with the effects of abiotic factors alone.

FIGURE 4 (a) Partial residual plots for predicted values for survival of female porcupines (*Erethizon dorsatum*) in Sandhill Wildlife Area between 1997 and 2018. Survival varied by age class, but also declined for all age classes with increasing snow duration. (b) Cumulative incidence functions for neonate porcupines for predation and non-predation mortality for years with snowshoe hares (*Lepus americanus*) and without hares in Sandhill Wildlife Area from 2012–2018. Predation mortality dropped by ~40% following the repatriation of hares. (c) Annual hazard rate estimates of neonate porcupines from cumulative incidence functions for predation and non-predation mortality in Sandhill from 2012–2018. Following hare repatriation, the predation declined, while non-predation mortality increased due to cold early spring temperatures
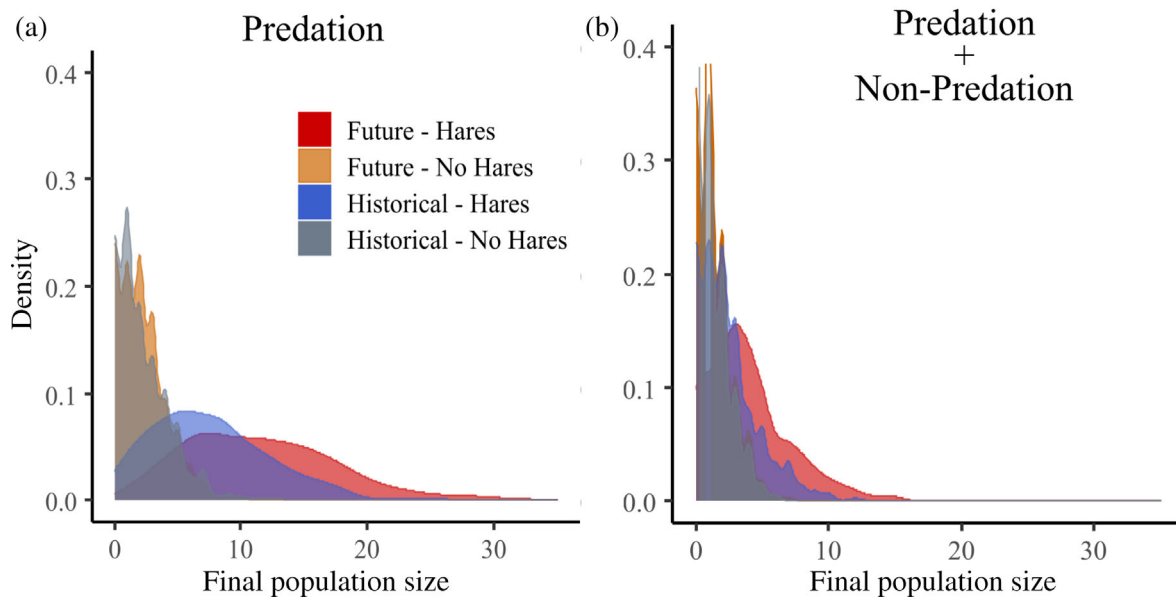
FIGURE 5 Simulated final population sizes from projected matrix population projections of female porcupines (*Erethizon dorsatum*) under scenarios with snowshoe hares (*Lepus americanus*) present or absent and climatic values representing future (2040–2059) and historic (1971–1990) conditions. Models included (a) only predation components of survival and (b) additive predation and non-predation components of survival. While all population models indicated population declines, the presence of snowshoe hares decreased the likelihood of extinction due to predation

DISCUSSION

Our experimental manipulation of a community module of vertebrates demonstrated that climate change had the potential to disrupt enemy-mediated indirect interactions and destabilize community and population dynamics. Repatriation of snowshoe hares altered the vital rates of alternative prey species as predicted, but predation pressure was unevenly redistributed between species and across age classes within species. The return of snowshoe hares altered predation rates and temporarily restored the biotic interactions that were historically present in this system, but that were recently lost due to the climate-related effects of camouflage mismatch, driving hares locally extinct. Restoration of these biotic interactions revealed a much stronger linkage between hares and porcupines than was observed for ruffed grouse, indicating a strong link between hare and porcupine population dynamics, while ruffed grouse may be only loosely linked to this community module or the relationship may be climate dependent.

We predicted that ruffed grouse would have weaker interactions with the community module than porcupines, but the lack of any effect of hare repatriation on adult survival or relative abundance, as indicated by the unabated downward trajectory in population counts, was unexpected. This disconnect between ruffed grouse and the other members of this community module could be due to differences in the importance of specific predators

on each species. Snowshoe hares and porcupines had considerable overlap in terrestrial predators—namely bobcat, coyotes and fisher (Wilson et al., 2019)—grouse predation was dominated by avian predators (Shipley et al., 2020). The increased mortality of grouse from predators that only weakly responded to population fluctuations of primary or alternate prey should result in weakened enemy-mediated indirect interactions between these species. Alternatively, it has been suggested that predation on eggs and chicks by predators of hares prior to the peak of hare abundance may drive the synchronization of population cycles (Keith & Rusch, 1989). Even though we did not directly measure changes in hatching rates or chick survival, we also did not observe an increase in drumming males from surveys in years following the hare translocation, which would have been one indication of increased recruitment. In fact, grouse populations continued their cycling during the almost 20-year absence of hares from Sandhill, albeit with the same recently dampened amplitudes observed across the southern portion of their range (Pomara & Zuckerberg, 2017). Finally, abiotic conditions, specifically snow depths suitable for burrowing and concealment, may have deteriorated past the point at which the effects of enemy-mediated indirect interactions can influence grouse population dynamics. The region surrounding Sandhill has experienced continual declines in snow depth, and average snow depths in this region now only

reach 15 cm (Notaro et al., 2011), the minimum depth necessary for snow burrowing, exposing grouse to prolonged periods of shallow snow, which has notable negative fitness consequences (Shipley et al., 2020). This increased climate variability has also been linked to rangewide declines in synchronous population cycles in grouse (Pomara & Zuckerberg, 2017). Grouse population dynamics may be tied to hare population dynamics and cycles in systems in which abiotic conditions are more stable, yet the linked population dynamics between grouse and hares reported in other systems appear to be absent along this trailing edge of range distribution.

Predation was the leading cause of mortality in neonate porcupines when hares were absent; following hare repatriation, predation of neonates declined by >60%. This inversion of hazard rates suggests an important indirect relationship between hares and porcupine mediated by predation from generalist predators. However, changes in predation rates among neonate porcupines did not alter the rates of overall survival and recruitment following repatriation. Instead, climate drove maternal condition, which cascaded to drive an increase in compensatory non-predation mortality. Climate can strongly affect porcupine population dynamics (Klvana et al., 2004; Mabille et al., 2010; Sweitzer & Berger, 1993); however, previous research has focused on declines in adult survival, due to increased predation during winters with increased snowfall (Mabille et al., 2010). Our results demonstrated that winter snowfall affects not only adult survival, but also neonate mortality via the effects of climate on maternal condition. Climate then, probably has conflicting effects for porcupines; warming winters decrease non-predation mortality and increase adult survival, yet the loss of snowshoe hares via climate-driven camouflage mismatch seemingly increased the predation mortality of porcupine neonates. Given these observed relationships, we propose that porcupine populations historically responded to indirect effects linked to snowshoe hare abundance, as well as to direct effects from winter conditions. Specifically, during the trough of hare cycles, porcupine neonates experienced high predation rates but, at the peak of hare populations, predation pressure on neonate porcupines was buffered. Concurrently, in mild winters featuring late snow initiation and warmer temperatures surrounding parturition, recruitment was sufficiently high to increase porcupine abundance, while in colder winters maternal condition declined as well as neonate survival even in the face of attenuated predation pressure. Therefore, we postulated that porcupines historically tracked hare population cycles, but that this synchrony in population dynamics is climate mediated.

The response of porcupine vital rates to hare repatriation reveals the importance of enemy-mediated indirect interactions for the porcupine–snowshoe hare relationship. Because of the positive response of porcupine vital rates to increases in hare abundance, it appears to be probably due to either an apparent mutualism or commensalism. Although the benefits of hares to porcupines is clear, the benefit of porcupines to hares remains unknown although, at low hare densities, porcupines may act as a buffer from predation, particularly from fishers. Apparent mutualisms are observed infrequently (Frost et al., 2016), but may be more likely to occur in the presence of cyclic population dynamics than in populations in which cycling is absent (Holt & Bonsall, 2017). Although snowshoe hare population cycling has been absent from this community module since the 1950s (Keith et al., 1993), the mechanisms that link these species together, namely a shared guild of predators, are still present. Moreover, the effect of hare repatriation resembled the dynamics that would be present in a population cycle, with a peak in hare abundance followed by a subsequent crash (Krebs et al., 1995; Wilson et al., 2019). The presence of an apparent mutualism matches the response expected from a community module that is dominated by generalist predators that switch between prey species as a functional response to abundance. Given that foraging for hares and porcupines requires different strategies (Powell, 1979), it is likely that prey switching is a conscious decision based on optimal foraging theory, rather than opportunistic predation. Prey switching can increase the likelihood of persistence in generalist predators along trailing range edges by decoupling them from a single prey species' population dynamics (Peers et al., 2014). This prey switching by predators has been observed elsewhere, with predation rates of alternative prey species increasing during the decline phase of the snowshoe hare cycle (Prugh, 2005). It provides a probable mechanism for the correlated population dynamics of many northern forest species to the snowshoe hare population cycle (Boutin et al., 1995) and highlights the broad impacts that the effects of climate change on snowshoe hares may have on this community at large (Prugh et al., 2018). Although we ultimately inferred prey switching from changes in the vital rates of prey species, future work could further explore these relationships by directly quantifying the shifts in predator diets or changes in predation rates of prey species in response to altered predator–prey assemblages.

Given the importance of biotic interactions linked to the now-extirpated snowshoe hare populations, it is unlikely that this community module will persist at this southern range boundary. The repatriation of snowshoe hares to Sandhill was short lived due to high predation rates linked to camouflage mismatch, revealing that climatic conditions are no longer suitable for their persistence (Wilson et al., 2020). All porcupine population projections

revealed a decline in population size, assuming a closed population within the study area; the projection with the highest ending population size represented the presence of snowshoe hares and warmer climatic conditions; a scenario that is extremely unlikely, given the irreconcilable relationship between shorter winters and hare presence due to camouflage mismatch (Wilson et al., 2019; Zimova et al., 2016). The weak effect of hares from our projection models was corroborated by the only slight increase in individuals observed during the post-translocation surveys. Moreover, while fishers alone are sufficient to suppress porcupine populations to low levels (Powell, 1993), this southern range boundary community also contains coyotes and bobcats, both of which can predate neonate porcupines (Mabille & Berteaux, 2014) and, to a lesser extent, adult porcupines (Prugh, 2005). Indeed, porcupine populations were increasing at Sandhill until the recolonization of fishers in the mid 2000s (Pokallus & Pauli, 2015), despite the absence of hares. Populations of porcupines in other regions have been driven to near extinction due to prey switching by predators when primary prey items become scarce (Sweitzer et al., 1997). Ruffed grouse, similarly, are likely to decline as snow conditions become less and less suitable. What the loss of these central, mid-sized prey species will mean for the predator guild, especially for fishers, is unclear. Fishers are specialized predators of porcupines (Powell, 1993), especially when hare populations are low (Bowman et al., 2006; Powell & Zielinski, 1994). Given this close link with porcupines and snowshoe hares (Powell, 1993), and the fact that this is a regionally recovering population, a lack of preferred prey is likely to incur important fitness costs on fishers and potentially limit their recovery along this southern range boundary (Kirby et al., 2018). It is possible that other less snow-adapted Carnivorans, such as bobcats and coyotes, will continue to increase in abundance, further altering the structure and dynamics of this community. In particular it is likely that diminished snow depths could cause a decrease in the survival of snowshoe hares by eliminating areas and periods of deep snow that allow hares to avoid predation by these less adapted predators, even before the effects of mismatch are apparent (Peers et al., 2020). Snowshoe hares, then, may act as a sentinel species in these systems; not only does their decline due to climate change indicate poor futures for other snow-adapted species, but the loss of snowshoe hares and their associated biotic interactions can indirectly contribute to population decline in other species.

Our experimental manipulation of a multi-prey, multi-predator community module along a southern range boundary suggests that there are unequal degrees of biotic interactions between alternative prey species, most likely to be due to slight differences in predator communities, which may drive population dynamics. We propose that these biotic interactions are likely to be the reason for previous community persistence; however, the effects of climate change have disrupted these interactions, altering vital rates and population dynamics of at least one alternate prey species (i.e., porcupine). We show that climate change has a range of effects, from direct and negative impacts on survival in snowshoe hares to direct benefits for adult porcupine survival. Furthermore, the indirect effects of climate change are driving a central prey species to regional extirpation and have eliminated an important enemy-mediated indirect interaction to alter recruitment in a trophically linked species. It is likely that climate has always played a role in these biotic interactions, but the increased variability and general declines in snow cover have played, and will play, an increasingly important role in determining the effect size of these biotic interactions. Although our experimental repatriation occurred in a limited geographic area, we propose that the observed implications of climate change, namely declines in snow duration, are present across the shared southern range boundary of this community module (Figure 1b) and that our results are applicable across this trailing edge range boundary. Furthermore, we propose that these observed changes may be present, even if more subtly (due to altered predator and prey interaction strengths), in northern portions of this shared geographic distribution and will only increase in strength as suitable climatic conditions continue to shift northward. The continuing loss of biotic interactions is likely to have repercussions throughout the community, potentially resulting in community disruptions as northern-adapted species contract and southern species expand their range northward.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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